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Female Homosexual Behavior in *Macaca Mulatta*

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Homosexual activity among adult females in a heterosexual group of rhesus monkeys (Macaca mulatta) *is documented and discussed. The mounter was usually in the follicular stage of the menstrual cycle and the mountee was in the ovulatory period. Activity during the luteal phase was low for all animals. Female mounting did not appear to be a preparation or substitute for heterosexual activity. Ritualized solicitation patterns among the females were intense and varied, strongly resembling those for heterosexual pairs. Dominance, partner preference, sexual stimulation, reproductive state, individual characteristics, and past experience are discussed in the framework of multiple factors influencing the homosexual relationship.*

KEY WORDS: homosexual; preference; solicitation; menstrual cycle; compatibility; primates.

INTRODUCTION

The purpose of this article is to describe and document female homosexual behavior in a heterosexual group of rhesus monkeys. The literature concerned with female mounting is scarce. Beach (1968) reviewed the literature to date, citing homosexual activity for 13 species of five different orders. Homosexual behavior in female primates has been reported for chimpanzees (Bingham, 1974; Yerkes, 1939), rhesus monkeys (Carpenter, 1942; Harlow, 1965; Sade, personal communication; Loy, personal communication), squirrel monkeys (Talmage-Riggs and Anschel, 1973), vervets (Struhsaker, 1967), pigtailed macaques (Tokuda *et al.*, 1968), Japanese macaques (Hanby and Brown, 1974), and stumptail macaques (Chevalier-Skolnikoff, 1974, 1976). Goy (1975) has reviewed

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the literature on homosexual behavior in both intact and hormonally modified laboratory animals.

Information regarding the hormonal state of the females involved in homosexual behavior is scarce. Documentation for several species supports the view that the animal mounted is generally an estrous female regardless of the state of the mounter. This appears to be true for chimpanzees (Yerkes, 1939), for rhesus (Carpenter, 1942), for cows (Hammond and Day, 1944), and for some female lions and domestic cats (Beach, 1968).

Michael *et al.* (1974) described the bisexual behavior of female rhesus monkeys. They found that female mounting of males was maximal at midcycle when the heterosexual activity of the pair was greatest. Individual preferences strongly influenced the frequency of mounting.

The following article will describe homosexual behavior among female rhesus monkeys in relation to their menstrual cycle. The term "homosexual" is used in reference to strong affectional ties involving courtship and physical contact between females. We stress Beach's hypothesis "that mounting behavior by females is a type of behavior which may be widely distributed throughout the class Mammalia. It may be further suggested that for many species such behavior is not abnormal, does not represent manifestations of 'sex reversal,' but is instead to be considered a normal element in the behavioral repertoire of the species" (Beach, 1968).

METHODS

The animals in this study were removed from a free-ranging colony of rhesus monkeys on Cayo Santiago, Puerto Rico, and transferred to Sabana Seca, Puerto Rico. They were held in isolation for 5 months, and the final group of eight adult females and two adult males was established in the spring of 1973. At this time they were housed in a 25- by 25-ft outdoor corral. Table I lists all animals, their sex, age, and reproductive history. Tubal ligations were done on five females to prevent inhibition of cycles by pregnancy.

Animals were observed daily from July 30, 1973, to February 2, 1974 (640 hr of observation). The following behaviors were recorded:

bout: This is approach behavior preceding the mount between two females including circling, jumping up and down, hide and seek, and other forms of solicitation.

kiss: Females touch lips or tongues, sometimes also ear-biting or touching each other's faces.

masturbation: This is self-stimulation of pubic area.

ventral hug: Two females wrap their limbs around each other and hug for 5–10 sec. A female may stimulate her own clitoris simultaneously.

Table I. Group Composition

Animal[a]	Sex	Born	Parity	
P2	Male	1966		
K6	Female	1965	Multiparous	
E8	Female	1965	Multiparous	Oviducts tied 4/6/73
X2	Male	1966		
2K	Female	1967	Multiparous	Oviducts tied 4/6/73
B1	Female	1965	Multiparous	Oviducts tied 4/6/73
4C	Female	1967	Nulliparous	Oviducts tied 4/6/73
6H	Female	1966	Multiparous	
HT	Female	1960	Multiparous	
ED	Female	1957	Multiparous	Oviducts tied 4/6/73

[a] All animals are listed in order of dominance rank.

clutching reaction: "the female turned her head around, backwards and upwards, to look at the face of the male. This was accompanied by vigorous lip-smacking and a reaching back with one hand to grab and pull at the hair of the male's head, shoulder, lower abdomen, thigh or leg" (Zumpe and Michael, 1968). This is used here in reference to two females.

pause: The female stops thrusting during the mount, arches her back, and stares into space.

heterosexual mount position: "the male clasps the female's waist with his hands and the backs of her legs with his feet" (Michael and Wilson, 1973). This is used here in reference to two females.

homosexual mounting position: "the mounter would climb on top of the mountee's shoulders with her hands and her hips with the feet . . . the mounter would then rub her genitals on the rump of her mountee" (Chevalier-Skolnikoff, 1974).

partial mount position: The mounter stands with feet on the ground and hands on the mountee's hips while rubbing or thrusting against the mountee.

sideways homosexual mount: This is a less coordinated homosexual mount where the mounter is perpendicular to the mountee.

mount refusal: The mountee may sit down or run away when solicited for a mount.

Dominance rank was determined by consistent win/loss in aggressive encounters. Heterosexual mounts were also recorded. Visual data were collected daily on menses and sex skin (scale of 1–4 by eye). Although the females were swabbed for verification, onset of menses in this text should be considered ± 1 day. Female mounts were recorded as single events, but only those which were closely spaced temporally are reported here. Single mounts which did not occur in series were not included in these data.

To examine the influence of ovarian hormones, the menstrual cycle was divided into three stages. The day of ovulation was estimated by backdating 14 days from the first day of menstruation. The follicular stage was considered to begin day 1 of menses and end 2 days prior to the estimated ovulation day. The ovulatory period was taken as the ovulation day, 2 days before, and 2 days after. The luteal period was the eleven days from the end of the ovulatory period.

Mean homosexual activity/ 2 hr period was examined as a function of menstrual cycle stage by analyses of variance. Units of analysis were observation periods for monkey pairs. Female mounting and ventral hugging were analyzed as combined homosexual activity. Both occur in series and involve the same animals. Females are also listed by pair to clarify individual relationships, and the nature of each type of behavior will be discussed separately.

RESULTS

Distribution of Homosexual Activity by Month

Seven of the eight females engaged in homosexual behavior. One pair (B1 and 4C) engaged in frequent ventral hugging series but were never seen mounting. Reciprocal mounting was observed in only one pair (E8/ED). Two adult males were present throughout the period, and often both homosexual and heterosexual activity occurred on the same day. A total of 113 heterosexual copulations to ejaculation were observed during the study period.

Table II shows the mean frequency of mounting activity for four pairs of females (mounter listed first) and ventral hugging for one pair (B1/4C) during the study period. This represents a total of 1561 mounts and 604 ventral hugs.

Table II. Mean Number of Female-Female Mounts by Month

	Pair						
Month	ED/E8	E8/ED	E8/2K	E8/B1	B1/4C[a]	Month means	Total mounts
Aug.	3.7	2.3	0.7	2.8	0.0	1.9	313
Sept.	1.3	0.4	6.4	7.0	0.0	3.0	451
Oct.	0.0	0.0	0.6	9.8	0.0	2.1	323
Nov.	0.2	0.1	0.0	4.8	4.8	2.0	254
Dec.	0.3	0.0	0.3	8.9	9.0	3.7	574
Jan.	0.1	0.1	0.3	1.3	6.9	1.7	250
Pair means	0.9	0.5	1.4	5.7	3.4		
Total mounts	178	89	252	1042	604		

[a]Homosexual activity is ventral hugging rather than mounting.

A pair by month analysis of variance for activity/2 hr period was done. Month was significant at the 0.03 level with mean mounts over 6 months, peaking in September and December. The difference among pairs was more significant ($p < 0.001$) and can be attributed to the high activity of pairs B1/4C and E8/B1. The effect of pair by month was also highly significant ($p < 0.001$). Three pairs restricted their mounting to 1 month, one pair to 3 consecutive months, and the most active pair maintained intense mounting throughout the study.

Female pairs not listed in Table II are K6/B1 and E8/HT. K6 was the dominant female, whose mounting abruptly ended when she became pregnant in the middle of August. The mounting between E8 and HT was restricted to 1 day in September.

Homosexual Activity in Relation to the Menstrual Cycle

Figure 1 shows the mean female homosexual activity averaged over five pairs across three states of the menstrual cycle. The average menstrual cycle

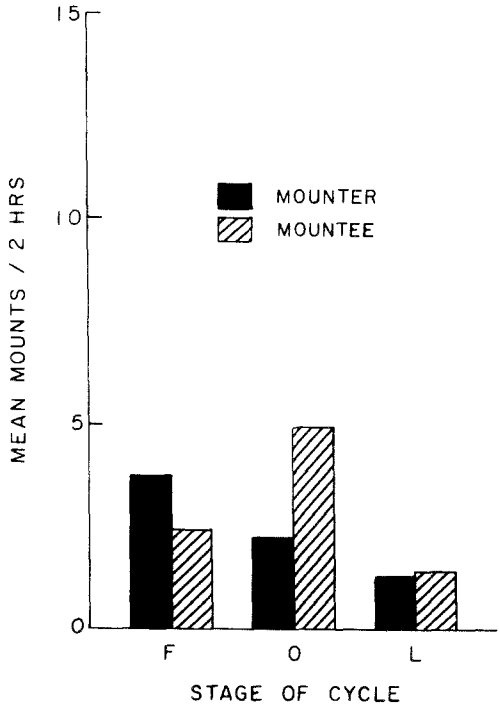

Fig. 1. Mean homosexual contact averaged over five pairs by stages of the menstrual cycle. F, Follicular; O, ovulatory; L, luteal.

length (in days) for each female active in homosexual behavior was E8:23.25, 2K:23.25, B1:28.50, 4C:25.50, HT:29.20, and ED:24.60. Stage by pair analyses of variance for homosexual activity/2 hr period produced highly significant results for the stage of the mounter ($p < 0.001$) and the stage of the mountee ($p < 0.001$). For the mounter, activity was highest in the follicular stage of the menstrual cycle. For the mountee, activity was highest in the ovulatory stage. Homosexual activity in the luteal period was consistently low for both.

Figure 2A–E shows the mean homosexual activity for individual pairs across three stages of the menstrual cycle. B1/4C was the only pair that engaged in ventral hugging and was not observed mounting. For pairs E8/2K and E8/B1 the *mountee* was most often in the ovulatory stage. 4C was also in the ovulatory stage when she was the recipient of ventral hugging. However, the reciprocal pair E8/ED showed higher follicular activity for the mountee, significant at $p < 0.086$. This pair contributed a relatively small number of mounts, but the significance is exaggerated because their activity is analyzed as two separate pairs depending on which female was the mounter. In the case of the *mounter*, the pattern of activity was more consistent. With four pairs the mounter was most often in the follicular stage. For E8/2K the mounter was in the ovulatory stage, but this deviation only approached significance ($p < 0.086$).

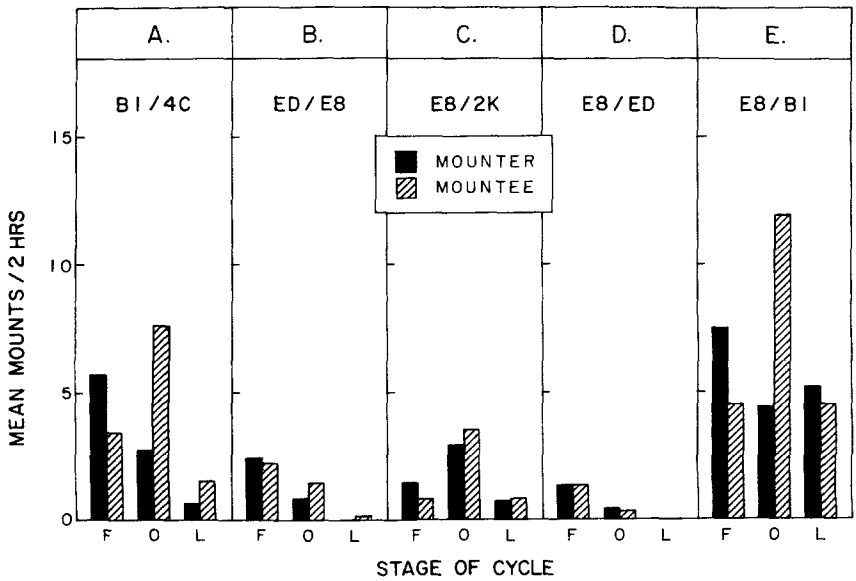

Fig. 2. Mean homosexual contact for pairs by stages of the menstrual cycle. F, Follicular; O; ovulatory; L, luteal. Pair B1/4C engaged in ventral hugging while the other four pairs mounted.

Pairs K6/B1 and E8/HT were not included in the analysis, although their mounting conformed to the group patterns described above. No data were available on K6's menstrual cycle because she became pregnant in August. However, the means across 6 months for B1 as the mountee are 0.62/2 hr (follicular stage), 2.30/2 hr (ovulatory stage), and 0.08/2 hr (luteal stage) for a total of 129 mounts.

E8 mounted HT only on September 23, 1973. The mounter was in the follicular stage and the mountee was in the ovulatory stage with a total of 12 mounts.

Mounting Positions

Figures 3–5 show the three basic mounting postures. The standard heterosexual position was common, although style varied within a series and according to the pair (Fig. 3). The homosexual position (Fig. 4) was most frequently used by E8, which was a particularly small animal. The heterosexual position may have been a necessary transition to climbing on top of the partner (just as one balances on the elbows before going into a headstand). Figure 5 shows the sideways position all pairs occasionally used.

Almost all mountees were seen to display the clutching reaction (Fig. 4). Sometimes the mountee stimulated her partner's clitoris while being mounted;

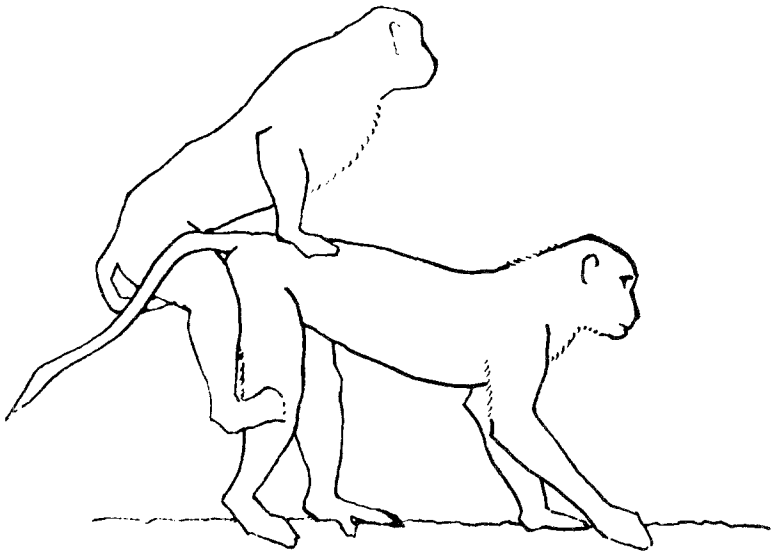

Fig. 3. Heterosexual mount position.

Fig. 4. Homosexual mount position.

self-stimulation by the mounter was common. Several females exhibited a pause after a series of mounts which resembled the male ejaculatory pause (Fig. 6). Obvious mount refusals were infrequent (total of 156). Only 6% of female mount attempts were rejected, in contrast to 29% of the heterosexual attempts at mounting. There appeared to be no correlation between the homosexual mount refusals and the menstrual cycle of either female involved.

Solicitation Patterns

Because of the nature of preliminary contact between two females, it was often difficult to determine the initiator of mounting activity. During mount intervals some animals sat together and groomed while others tended to separate. Mount intervals ranged from 5 sec to 1 min but seldom longer. Females solicited mounts by presenting, pulling tails, jumping up and down, or forcing another

Fig. 5. Sideways homosexual mount.

animal into position. Partners had favorite places in the corral to mount. All of the consort pairs showed following behavior and tended to be in motion in the cage at the same time.

Bouts preceding mounts varied in duration and intensity but almost always included several of the following behaviors: (1) "Present and run" was initiated by either female, and it resulted in pursuit or the sequence was repeated several times. (2) "Follow the leader" alternated between which female led and which female followed. (3) "Kiss and run" was initiated by female B1. She walked up to another female, quickly rubbed noses, touched lips, and ran away. Sometimes her partner followed and sometimes she ran away. Other times her partner would grab her ear and pull her head around to nuzzle in the same fashion. (4)

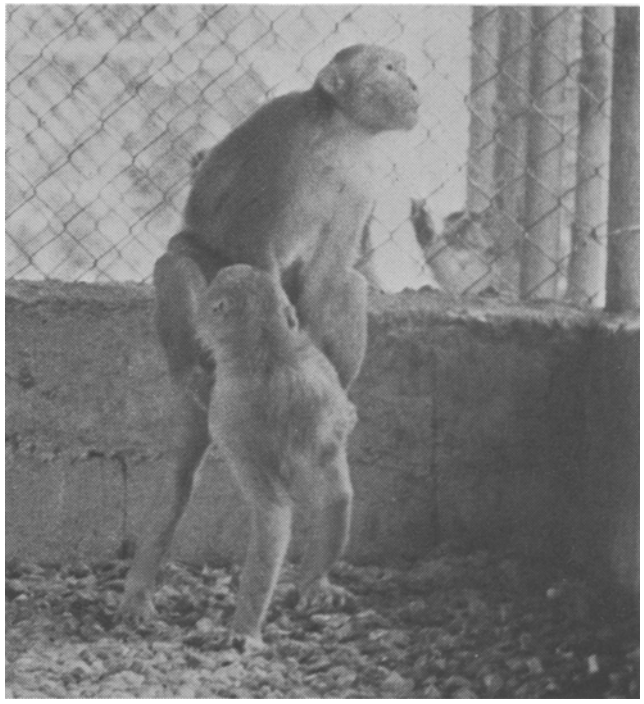

Fig. 6. Female-female mount with mounter exhibiting a pause similar to the male ejaculatory pause.

"Lipsmack and circle" was a frequent occurrence prior to the establishment of a consort. One female circled another lipsmacking and making smaller and smaller circles each time. This usually led to a long game of "hide and seek." (5) In "hide and seek" the females took positions on either side of a tree and peeked at each other, moving slowly around the tree and keeping just outside each other's reach (Fig. 7). There was also a whole series of brief maneuvers, including running up to another female very suddenly, hitting her gently in the face, and running away again, simultaneous tree-shaking, pulling each other's ears and tails, pacing together, and brushing past each other without stopping.

Threat gestures appeared to be a very effective means of getting attention. Females constantly solicited each other's support in threatening the observer, threatening other animals, or simply threatening in an arbitrary direction with no apparent recipient. There was a portion of seemingly "unwarranted aggression" which drew the preferred female away from another activity. Dis-

Fig. 7. During homosexual courtship, females engage in a game of hide and seek.

placement of another animal was also a useful means of gaining access to the preferred female.

Dominance and Preference

Dominance was reflected in the homosexual relationship in that the mounter was usually the more dominant female; the only exception was the reciprocal mounting between females E8 and ED (lowest-ranking female in the group). In other aspects of homosexual behavior dominance was often suspended. In all pairs either female initiated contact and mounting, and high-ranking females frequently solicited mounts by presenting to subordinate animals. Subordinate females threatened higher-ranking females, especially with the support of the consort partner, and females threatened each other during the approach with total disregard for rank. Female E8 (second-ranking female) also yawned sometimes during mounts, a gesture often attributed to males during dominance displays.

The females were competitive among themselves for E8's attention. E8 showed a strong preference for female B1 even when she was not in the ovulatory stage. This preference resembled that described for certain heterosexual pairs which maintained almost constant contact (Herbert, 1968). Animals which were denied access to the preferred partner paced the cage or threatened others to gain attention. The amount of direct interference was dependent on rank, but a subordinate animal could threaten a female above her with the support of the consort.

Homosexual pairs were also directly affected by simultaneous heterosexual activity. E8's preferred female was also a favorite with the dominant male. When female B1 was with the dominant male, E8 had difficulty gaining access to her and used many attention-getting devices to draw her away. Sometimes the female preferred the homosexual activity and left the male of her own accord. Other times she stayed with him or he chased away the intruder. It appeared that the females were aware of each other's movements so that they could cause or avoid an encounter. Access to the preferred partner was always difficult if she was in the company of the dominant male or female.

Female 2K was another example of how homosexual pairs were affected by heterosexual activity. Female 2K was a favorite with the subordinate male and also active in homosexual mounting with E8. This was important for two reasons. First, E8 was dominant to this male so that she did not have the difficulty gaining access to 2K that she had with B1 and the dominant male. Second, this male was the same one that E8 preferred for heterosexual activity so that the two females competed for his attention. At times females did show preference for each other over heterosexual mounting.

B1 and 4C Ventral Hugging

B1 and 4C were seen ventral hugging from November through January (Fig. 8). They also engaged in heterosexual mounting, and B1 mounted with female E8. B1 clearly stimulated her clitoris on the ground as she hugged 4C. 4C showed no obvious signs of self-stimulation, although she was receptive to contact with her partner.

B1 usually initiated contact by badgering 4C. This included jumping up and down in front of her, pulling her tail, displacing her each time she sat down, and threatening her if she was with a male so they could resume contact. These females maintained a favorite corner of the cage for activity. They usually threatened observers or other animals before hugging, then clasped each other for 5–10 sec. Intervals between hugs lasted 10 sec while the females appeared to ignore each other. B1 was also seen ventrally hugging the male infant of female 6H. She simply held the infant to her chest briefly, groomed him, then hugged again.

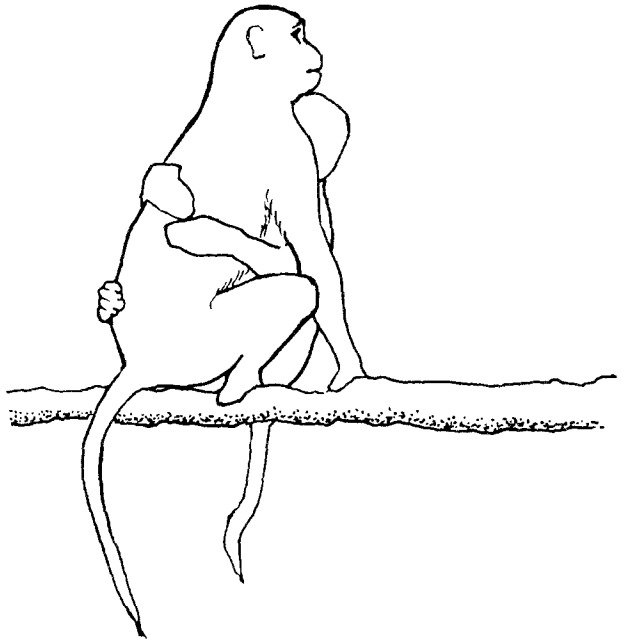

Fig. 8. Position for ventral hugging.

Individual Characteristics and Idiosyncratic Behavior

There were some forms of solicitation which involved other members of the group. One pattern developed after females E8 and B1 had been mounting for several months. B1 began to follow sixth-ranking female 6H. As E8 would draw near the pair, B1 would hit 6H; 6H would run away and B1 would present to E8 and be mounted. Following the mount series B1 would return to 6H and the sequence was repeated. 6H began to avoid contact with B1.

B1 also solicited 6H's company during masturbation sessions. B1 repeatedly joined 6H, groomed her briefly, then pulled away and rubbed her own clitoris on the wall for 5–10 sec. B1 was the only female seen stimulating herself when she was alone.

Several activity patterns particular to E8 should be mentioned. As the mounter in almost all the homosexual activity, she often displayed motor patterns typical of male rhesus during the breeding season. She carried her tail curled in the form of a question mark and displayed the typical male muzzle-up to other females during approach. After a series of mounts she also exhibited a pause similar to the male postejaculatory pause (Fig. 6). E8 frequently frowned while mounting and occasionally brushed her hand quickly between her legs before mounting.

During homosexual activity aggression from other members of the group was minimal. On a few occasions one of the males broke up the female mounting to gain access to one of the females. Several times the dominant male charged a pair and they fled to separate corners of the cage.

All females involved in homosexual mounting had extremely regular and somewhat short menstrual cycles except for female B1. Females 2K, B1, and ED copulated with males throughout the entire study while 4C, 6H, and E8 confined most of their heterosexual activity to December and January. Heterosexual activity was highly concentrated during the ovulatory stage but not restricted to that stage for preferred females 2K and B1.

DISCUSSION

In an attempt to understand homosexual activity among nonhuman primates several theories have been offered based on the limited data available. It is generally agreed that homosexual mounting facilitates training for adult roles and heterosexual relationships. The persistence of mounting behavior in adulthood among many mammals suggests that this is only a partial explanation. We found that, simultaneously with heterosexual activity, bonds between females (E8/B1 and B1/4C) were maintained or intensified (See Table II).

In a group of squirrel monkeys, Talmage-Riggs (1973) concludes that "homosexual behavior observed in this group deprived of physical contact with

males for two years was probably an attempted substitution for heterosexual mating." Conaway (unpublished) saw high levels of homosexual activity in a heterosexual group of squirrel monkeys during the breeding season. Female mounting has also been observed for *Macaca arctoides* (Chevalier-Skolnikoff, 1976). She suggests that watching heterosexual mounting is a strong stimulus for homosexual behavior, but there is no indication in this study that either relationship was an immediate stimulus for the other.

Dominance has also been correlated with female mounting in monkeys. Zuckerman (1932) related female mounting directly to dominance, while Kempf (1917) added the advantage of sexual stimulation for the mounter and the temporary increase in social status for the subordinate animal. Both acknowledge a preadult stage when homosexual mounting is common. Talmage-Riggs (1973) notes that "unlike aggressive behaviors cohesive encounters were not as directly related to dominance hierarchy. There was a tendency for the lower ranking female not to initiate hugging with close rivals." Wolfheim and Rowell (1972) state that in talapoin monkeys "Both males and females may mount males or females. Between females the position does not seem to be related to rank order, except that the higher ranking female of a pair usually mounts first in a series of mounts on reunion." Anthoney (1968) reported that the mounting of females by females of higher rank was common in *Papio cynocephalus.*

The dominant female in this study occupied a firm position in the group. She never interfered with any homosexual activity even though she was actively mounting before she became pregnant. This could be due to the fact that the pregnancy inhibited her motivation to mount, as in the luteal phase, or due to the stability of her role as the dominant female. The only reciprocally mounting pair ranked second and eighth in dominance.

The subordinate animal may be required to respond to a mount solicitation. Sometimes low-ranking females resisted mount attempts by pulling away or assuming an incompatible posture, but dominant animals were also uncooperative. This may be part of the courtship and not indicative of rejection since resistance only increased the activity of the pair. This supports the theory that the mountee is selected because she is sexually receptive and more likely to be cooperative.

Beach (1968) presents evidence for females of many mammalian species that the mountee is generally in a state of sexual receptivity while the mounter is not estrus. Chevalier-Skolnikoff (1974) reports for *M. arctoides* that the mounting female was never in estrus and the animal mounted only rarely. As she has noted, stumptail monkeys may engage in sexual activity more independently of hormonal cycles than other primate species. Since there is little external sign of estrous in stumptails, it is difficult to verify estrus related to time of ovulation without vaginal slides.

However, Hanby and Brown (1974) found that female-female mounting in Japanese macaques was mainly an adult female activity which definitely

seemed to be dependent on hormonal factors. They concluded this because female mounting increased at 3½ years of age and because female-female mounts were restricted to the breeding season.

Our study indicates that homosexual activity is usually highest when the mounter is in the follicular stage and the mountee in the ovulatory stage of her menstrual cycle. Nevertheless, strong bonds between females are not totally bound by endocrine factors.

The mounting female can achieve sexual stimulation by rubbing her clitoris against her partner, by self-stimulation, or through manual manipulation by the mountee. It is more difficult to assess sexual arousal for the mountee. However, when these same females engage in heterosexual copulations, the female is usually in the ovulatory period. Heterosexual series mounts occur during both the follicular period and the ovulatory period, but all activity is low during the luteal phase (Akers, in preparation).

As is true of stable heterosexual relationships, homosexual activity is not restricted to the mountee's ovulatory period (Loy, 1970, 1971; Akers, in preparation). Those pairs that persist in mounting throughout the menstrual cycle may indicate strong bonds not completely bound by endocrine factors. Since there is no estrus synchrony in this group, strong preference for a certain partner naturally results in mounting out of phase. Still the intensity and duration of these relationships are clearly influenced by hormonal change, and it is significant that the dominant female ceased mounting both with males and with females after she became pregnant.

It should be remembered that female mounting reported here did not occur in aggressive contexts. This is also true for Japanese macaques (Banby and Brown, 1974) and stumptail macaques (Chevalier-Skolnikoff, 1976). Chevalier-Skolnikoff also states that females with close affectional ties tend to engage in mounting, which is the case in the present study. In the present study, single mounts which appear to pacify an agitated animal are as common among males as females and are not included in this report. In homosexual and heterosexual consort pairs the status of the subordinate animal often is temporarily raised, but there is no evidence that these relationships have any effect on the dominance hierarchy outside of this context.

Goy and Goldfoot (1975) hypothesize that "there appears to be an inverse relation between the sexes with respect to bisexuality; thus, for a given species, the greater the bisexuality of the male, the less the bisexuality of the female, and *visa versa.*" They attribute this condition to early endocrine stimulation and suggest that the male rhesus is more inclined to bisexuality than the female. There are several ways of interpreting these data.

We have described female homosexuality which demonstrates the hormonal influence and cannot be confused with routine dominance interactions. However, the time spent in soliciting is much greater than that spent in actual physical contact, and strong affectional ties may also be a vital determinant

of the bonds which develop. The homosexual relationship appears to allow for the expression of many behaviors which are not masculine or feminine. Individual approaches to affection, preference, sex drive, and play behavior are reflected which may lack an adequate outlet in this group structure. In sharp contrast to the pyramidal age structure of the free-ranging populations, this study group consisted only of adult males and females and one male infant. The more usual opportunity for interaction between females and juveniles was eliminated in this captive group. Naturally, captivity can exaggerate behaviors which might be less frequent in the wild population.

By describing the homosexual relationship as a sexual one we neglect the possibility that strong bonds between females may be no more sexually motivated than stable heterosexual pairs for human or nonhuman primates. Sexual gratification may be a fringe benefit of a relationship that develops for a variety of reasons. Factors to be considered in attempting to understand homosexual behavior are as varied and complex as those for heterosexual bonds. In both cases, the duration and intensity of the relationship depend on the combination of animals. In either case the ties which develop are influenced by individual characteristics and experience, familiarity, affection, group composition, dominance, and hormonal fluctuations.

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